

## A COMPUTER SIMULATION STUDY OF MARK-RECAPTURE METHODS IN ECOLOGY

### 1. Means and empirical standard deviation from four models

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**ABSTRACT:** A Fortran computer program is described which simulates an animal population (with births and deaths) subjected to mark-recapture study. All parameters of the study can be specified. The population is estimated by the models of Lincoln, Schnabel, Bailey and Jolly, and mean values and empirical standard deviations are derived on the basis of twenty replications of each set of experimental parameters.

#### INTRODUCTION

The use of marks on animals to aid the study of their biology is a long-established one. Izaak Walton, in 1653, relates that Sir Francis Bacon attached 'ribands' to young salmon so they could be identified on their return. Marking is often used for the estimation of population size, and a great deal of sophistication has now been brought to the mathematical models used in making such estimates (Cormack 1968).

Considerably less attention has been given to the testing of these models on known populations: such studies have usually involved the comparison of several models on a single population, as, for example, Parr's (1965) study of a population of dragonflies using five models. Phillips and Campbell (1970) used four models on a closed population of whelks on a rocky shore platform.

Manly (1970) simulated populations subjected to mark-recapture methods on a computer, and obtained data on the behaviour of four estimation models. Later (1971a) he examined the behaviour of the variance estimates produced by the method of Jolly (1965) by simulation methods. More recently, other aspects of Jolly's method have been examined (Cormack 1972, Manly 1971b, Carothers, in press), and these are discussed more fully below. A very useful bibliography of mark-recapture methods has been compiled by Anderson (1972); comprehensive discussions are given in Robson (1969) and Seber (1972). White (1971a & b) supplies a Fortran computer program which will handle estimation by Jolly's (1965) method.

Models of mark-recapture estimation are based

on a series of assumptions about the population under study. The accuracy of the estimate will depend to a large extent on how closely these assumptions are met, and on the sensitivity of the particular model to each individual assumption. Thus apart from *sampling* errors, there are also *biological* errors in the estimation process.

The assumptions are as follow:

1. The marking method does not impair the animal functionally or behaviourally.
2. Marks are permanent, unalterable, and accurately decipherable.
3. The return of marked animals into the population does not alter its spatial structure.
4. All animals are equally available for capture, irrespective of
  - (a) mark status (i.e. whether marked or unmarked)
  - (b) age, sex or other group existing in the population (whether distinguishable or cryptic) (i.e. each group is sampled in the same proportion as it occurs in the population)
  - (c) previous capture history (i.e. being captured neither increases nor decreases the probability of an animal's being recaptured subsequently).
5. All parts of the habitat have an equal chance of being sampled.
6. Sampling is carried out in a discrete period of time which is small compared with the total time of the study.

The following assumption is also said to hold for the Lincoln Index and Schnabel models:

7. The population is either closed, i.e. there is

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neither recruitment (births and immigration), nor losses (deaths and emigration) to the population of the period of study; or else recruitment and/or losses can be independently assessed and allowed for.

Assumptions 1 and 2 can be examined by independent laboratory and field studies. It does seem probable, however, that some marking methods must impair the recipient: for example the more radical toe-removal methods used to code small mammals. Such methods are undoubtedly permanent, and unless the animal accidentally loses another toe, are accurately decipherable. Paint-marks used on insects can chip off, or colours can fade. Such marks can be field-tested by using two (or more) separate, independent marks on each animal, thus checking on the long-term reliability of each system. Marking systems should not be of such complexity that human error in reading marks becomes a factor. This can be assessed by having more than one observer independently decipher each mark.

Assumption 3 is a procedural matter, in the hands of the researcher—it requires deep thought into the *timing*, as well as the placement, of releases. It is probably also advisable to release animals at the point of capture, and not to rely on dispersal from one or a few release points.

Before examining the other assumptions more fully, it is necessary to consider the process of estimation (Cormack 1972). The population contains a sub-population of identifiable individuals, the members of which bear either unique, individual marks or a code-mark which identifies the date (and perhaps other information such as place) of marking. It is assumed that the characteristics of this sub-population are known to the biologist (e.g. its size), and that any changes are also known or can be detected (e.g. additions and deletions from the sub-population). Most importantly, it is assumed that changes estimated from this sub-population of identifiable individuals are an estimate (whose accuracy can, in turn, be estimated) of processes in the population. Thus, for each capture-recapture cycle, estimates are

made of sampling intensity  $\hat{p}_i$  (in the notation of Cormack 1968)\*, birth rate  $\hat{B}_i$ , and probability of survival  $\phi_i$ .

From these, further estimates may be made for the overall population, e.g.  $\hat{N}_i = n_i \hat{M}_i / m_i$  ( $= n_i / \hat{p}_i$ )\*. Cormack (1972) points out that to solve the estimation formula it is necessary to know (or to directly estimate) one and only one of the sets  $M_i$ ,  $p_i$ ,  $N_i$ ,  $\phi_i$  or  $B_i$ ; knowledge of the set  $\phi_i$  or the set  $B_i$  must be supplemented by knowledge of one  $M_i$  or  $N_i$ . From this logical base all the models of mark-recapture estimation can be interpreted. Thus Jolly's (1965) and Seber's (1965)† maximum likelihood solution of the estimation of the marked sub-population is

$$\hat{M}_i = m_i + s_i z_i / r_i$$

where  $z_i$  is the number of animals marked before the time of the  $i$ th sample, but not included in it; and  $r_i$  the number of the  $s_i$  animals released at the  $i$ th period that are seen later. Thus the second term is an estimate of the number of marked animals alive but unseen at the  $i$ th sampling period, and  $m_i$  is the number actually seen (Jolly 1965).

On the question of availability of animals for capture, detailed observation may show whether this is likely to be violated. If certain individuals or groups are more conspicuous in the population, their probability of capture may be biased (positively or negatively). Conspicuousness may be physical (e.g. bright plumage or bizarre ornamentation on birds or insects, as in sexual dimorphism), or behavioural (e.g. due to dominance hierarchies or division of labour (Golley & Gentry 1964, Wilson 1971)). Cormack (1972) shows that the catchability of these individuals is higher at the start and thus average catchability declines during the course of the project. However, if the catching method discriminates *against* conspicuous individuals (e.g. by personal bias of an operator, or by a size-filter effect of a trap), the reverse or a different bias may arise.

Another aspect of this same question is trapping history, and trap-proneness and trap-shyness

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$$p_i = m_i / \hat{M}_i$$

where  $m_i$  is the number of individuals of the sub-population of marked animals  $\hat{M}_i$ , sampled on the  $i$ th occasion

$$\hat{\phi}_i = \hat{M}_i + 1 / (\hat{M}_i + s_i - m_i)$$

where  $s_i$  is the number of marked animals released after the  $i$ th sample.

$$\hat{B}_i = \hat{N}_i + 1 - \phi_i (\hat{N}_i + s_i - n_i)$$

where  $n_i$  is total sample size on the  $i$ th occasion,  $\hat{N}_i$  is the estimated population at time  $i$ .

† Jolly (1965) and Seber (1965) produced the same solutions to the problem of mark-recapture estimates of populations, under a stochastic model; Jolly's treatment, however, is more generalized, and is referred to hereafter.



are well known to workers on vertebrate animals. (The effects of training on invertebrates should not be overlooked, however.) Orians and Leslie (1958) provide a test for random recapture of individually-marked animals. One further situation to be avoided is the use of baited traps in, for example, studies of social insects where recruitment of a specialized group of foragers occurs when a single successful forager has returned to the nest (Wilson 1971). The effects of bias in catchability is reflected in the estimate of  $M_i$ ; this is discussed for the Jolly model by Cormack (1972) and Carothers (in preparation).

The bias in estimates caused by differences in survival is discussed by Cormack (1972). In the Jolly method, general survival is estimated for each period; in others (e.g. Fisher & Ford 1947) an overall estimate is made for the entire period, and this may lead to serious bias. The most serious effect of differential survivals will occur when this effect is associated with marking. The situation can be allowed for if the effect is assumed to occur only after the first capture (and marking), and to last only until the next recapture (the type I loss of fisheries biologists) by considering two sub-populations of newly-marked and mature-marked individuals. The estimates then follow logically (Cormack 1972). Manly (1971b) discusses the same situation for the case where animals bear individual marks—he develops a method for analysing type I losses, as a special case of Jolly's estimator (if the animals die while being marked, this is allowed for in the Jolly model).

Assumption 5, that all parts of the habitat have an equal chance of being sampled, rests on the design of the sampling program, which is excellently covered in specialized texts. Planning for efficient sampling will also ensure that assumption 6 is met—that sampling is carried out in a relatively short, discrete time interval.

The present paper presents the results of a computer simulation study in which four estimation models were examined. The selection of these models was influenced by their being used or under consideration for use in studies of the Desert Biome Program of the US/IBP Analysis of Ecosystems. As mark-recapture studies were to be used for a wide range of taxa, a comprehensive, realistic model of a population subject to such study was required. This paper describes the computer model and the first set of results obtained from it, for idealized populations which completely meet the assumptions discussed above.

## METHODS

Idealized animal populations, being studied by mark-recapture methods, were simulated by a

program written in Fortran IV called **SYNPOP**. This was run initially on an IBM360/50 computer at New Mexico State University, Las Cruces, New Mexico, and later adapted and expanded for a Burroughs B5500 computer at Monash University.

The basic outline of the program is relatively simple (see Fig. 16). An array '**POP**' is set up, and a number of places in the array—corresponding to the starting or 'seed' value of the population—are set equal to 99, which identifies new-born animals. They retain this value unless they are captured (see later) or killed (when their value becomes zero).

The population then goes through a series of cycles of deaths, births and sampling, the number of cycles being specified by the experimenter. He also specifies death and birth rates, either as probabilities or as fixed fractions of the population at the start of each day, and these may apply uniformly throughout the period of the experiment, or may be specified (independently) in particular cycles. The experimenter may also specify that births should exceed deaths or vice versa; and finally, he may nominate a probability that animals captured in samples, are killed in handling and marking, a common experience in entomological work.

The selection of which animals are killed, and which are sampled (as well as other events of a stochastic nature), is controlled by a pseudo-random number generator which supplies numbers within the population bounds. The appropriate process is then applied to the animal occupying that position in the population array '**POP**' (after a check that that animal is in fact, 'alive'). The pseudo-random number generator has been carefully tested, and supplies a random sequence of real numbers, uniformly distributed in the long run between 0 and 1. This number is multiplied by the standing population size at the time to obtain the order number of the animal selected. The experimenter supplies a set of six random numbers, obtained from one of the published tables (e.g. Rohlf & Sokal 1969) to seed the generator separately for each process.

In each population cycle the population undergoes a death phase first, followed by a birth phase. The numbers of deaths and births are specified by separate sub-routines according to the experimenter's instructions.

**DEATH:** In the death phase a random number is generated and this animal is examined. If it has a value of 99 its death is recorded; if its value indicates it is a marked animal its mark is recorded in another array '**WLDKIL**'; if its value is zero, this indicates the animal in this array position is dead, and it is ignored for the moment.

In the first two cases the value in the array 'POP' is set to zero, and another random number is obtained. This procedure continues until the required number of deaths has occurred.

**BIRTH:** In the subsequent birth phase the array 'POP' is checked through and zero spaces are changed to 99 (new-born animals) until the specified number of births has occurred. If there are insufficient zero spaces in array 'POP', its upper bound is increased with new-born animals.

**SAMPLING:** The array 'POP' is then sampled. Animals are again selected by the random number generator; each is examined and, if dead, another is selected. If the animal has not been previously captured (i.e. equals 99) its value is set to 1. Previously marked animals thus have marks other than 0 or 99—at the start of each cycle, all previously marked animals have their value multiplied by 10 so an animal caught in the previous cycle would, on capture, have a mark of 10. A 1 is then added, and this animal's mark is changed to 11. Similarly, an animal carrying a mark 10101 would have been marked in the present, last but one and last but three cycles. The marks of such previously captured animals (recaptured during sampling) are noted in an array 'MARX', for later printout, and the mark is analysed by the main program (for the Lincoln Index and Schnabel estimators) and by the sub-routines BAILEY and JOLLY for the Bailey Triple Catch estimator (Bailey 1951, 1952) and Jolly's Stochastic estimator (Jolly 1965).

Finally, a random number is drawn; if this is less than the specified probability of an animal being injured during marking, this animal's mark is transferred to another array 'SMPLDD', and its position in the population array 'POP' is set to zero (animal dead). This cycle is repeated until the required size of sample has been obtained.

This sequence of deaths, births and sampling is thus carried out on the population for as many time periods as the experimenter may select. Such a sequence, representing a population over a period of time, is herein referred to as an experiment. For each set of parameters—seed value, birthrate, deathrate, sample size, number of time periods—the experimenter may also nominate the number of times he wishes this experiment repeated independently (or replicated). This is done on the parameter card (see facsimile of printout). For each replicate, the experimenter supplies a new set of six random numbers, as mentioned above, which seed the pseudo-random number generator for probabilistic death or birth functions, random selection of animals for death and capture, variation in sample size, and whether an animal chances to be killed during marking.

Finally, a sequence of different experiments may be carried out in a single run.

The program used here consists of a main program which acquires data (the parameters and random number seeds) and carries out the actual manipulation of the population. There are a series of sub-routines and functions, as follow:

Sub-routine	SAMPLE—calculates sample size
„	BIRTH—calculates number of new animals in each cycle
„	DEATH—calculates number of deaths in each cycle
Function	RNUM—supplies random numbers, $n$ , ( $0 \leq n \leq 1$ )
Sub-routine	LINC—estimates the population size by the Petersen or Lincoln Index method
„	SCHNAB—estimates the population size by Schnabel's method
„	BAILEY—estimates the population size by Bailey's 'triple-catch' method
„	JOLLY—estimates the population size by Jolly's stochastic method
„	LINCSTM—collates the results of the successive Petersen estimates over the several replicates, supplying a mean and standard deviation for each cycle
„	SNBSUM—collates results for Schnabel estimator as above
„	BALSUM—collates results for Bailey estimator as above
„	JOLSUM—collates results for Jolly estimator as above
„	PRINT—organizes output from the four collating sub-routines
„	TRUVAL—prints out summary of true values of populations at the end of each sequence of experiments

A facsimile of the main program and the sub-routines (excluding the last six, book-keeping sub-routines) is reproduced as an Appendix to this paper.

Output is produced on the line printer for each experiment. After identification, all the parameters for the experiment are given. Optionally, for each cycle, there is a summary of population size, number of births and deaths, and size of sample drawn, and the marks of marked animals caught in samples, of those killed in marking, and of those killed 'in the wild' are displayed. (As a further option, the whole population may be



printed out also, but this obviously consumes a lot of paper and is only used in special cases.) The number of animals marked and unmarked, and the percentage marked, is printed, for each cycle.

At the end of each experiment, the four sets of estimates of the population, together with other relevant statistics (e.g. estimated standard deviation) is printed. The unbiased forms of the estimators are used to obtain population size (Cormack 1968).

After all replicates of the experiment have been completed, summaries of the estimates for each model are printed, and a table of the actual population values in each replicate.

## RESULTS

Thirteen separate experiments were performed; each had different birth and death rates, as summarized in Table 1. Each experiment was replicated 20 times. The starting value for each population was 1,000, and the sample size  $100 \pm 10$ . The probability that an animal was injured during capture and marking was set at three per cent. Thus experiment 1 to 3 were with stable populations (except for the slight loss due to injury) where birth and death rates were equal. In experiments 4 to 7 the populations undergo simple growth or decay; in 8, 10 and 12 the populations go through a growth and then a decay cycle; and in 9, 11 and 13, the sequence is reversed.

The results for each experiment are summarized graphically (Figs. 1-13). The upper half of each graph shows the results obtained in two replicates, chosen at random, by each of the four estimator models. Below each of these the mean  $\pm$  one

standard deviation for all twenty replicates is shown for each sampling period. The use of the standard deviation as a measure of spread is justified if all replicates are plotted (for example, as in Fig. 14, for Jolly estimator in experiment 1) when it will be seen that 60-70 per cent of points lie within the limits of  $\pm$  one standard deviation. Superimposed on each graph is the actual trend line of the population, for comparison.

Fig. 15 shows the proportion of the population bearing marks at the end of each sampling period, for each experiment.

## DISCUSSION

Of the four estimation models used, two (Lincoln Index and Schnabel) are based on the assumption that there are no gains (through birth and immigration) or losses (by death or emigration) to the population, while the other two models purport to account for these. The mathematical background (including other assumptions) to these is discussed by Cormack (1968) and Southwood (1966); both authors cite a large number of references to field application of these methods, the former being biased toward fisheries applications and the latter toward entomological studies. (Readers should note that Southwood has a number of errors in his mathematical formulae—marring an otherwise excellent discussion.)

Such theoretical models allow biologists to obtain estimates of population size and other population attributes from mark-recapture studies, together with estimates of the standard deviations. Hopefully, this allows the biologist to place confidence intervals on his estimate(s) of the population: that is, he states that he has, say, 95 per cent confidence that the true size of the population lies within (approximately) two standard deviations of the estimated value. Thus Cormack (1968) cites examples of the use of Jolly's (1965) stochastic method, and quotes percentage 'accuracies' achieved.

Models, however, are predicated on assumptions, as are the statistical methods used to elucidate the models. Is it possible that the assumptions are not justified, in which case either the estimated population size, and/or the associated variance estimate, could be misleading? To date, the only way of testing this proposition was by the comparison of different models. If the answers did not correspond, the particular worker made a subjective judgment in favour of one or more models (e.g. Parr 1965).

Manly (1970) approached this problem by computer simulation of a mark-recapture system. Unfortunately the method he used is not clearly

TABLE 1

Experiment	Periods	Birthrate	Deathrate
1	All	0	0
2	All	0.10	0.10
3	All	0.20	0.20
4	All	0.10	0.0
5	All	0.0	0.10
6	All	0.20	0.10
7	All	0.10	0.20
8	1-5	0.10	0.0
	6-10	0.0	0.10
9	1-5	0.0	0.10
	6-10	0.10	0.0
10	1-5	0.20	0.0
	6-10	0.0	0.20
11	1-5	0.0	0.20
	6-10	0.20	0.0
12	1-5	0.20	0.10
	6-10	0.10	0.20
13	1-5	0.10	0.20
	6-10	0.20	0.10

described in the paper. Each population starts at zero and grows over a period of ten 'days'. At the start of each day, births occurred (either 25, 50, 75 or 100), and at the end of each day, deaths occurred, in accordance with one of twelve life tables. Sample size varied from approximately 10 to 95 per cent. There were 96 populations and each was sampled, independently, ten times during each of the last five days giving ten independent sets of estimates of the population. Estimation models used were Fisher and Ford (1947), Jolly (1965) and Manly and Parr (1968).

Manly analyses the results obtained in terms of 'percentage relative bias' (i.e. [estimate-true value]/true value, as a percentage) and mean square error. He found that when its assumptions were met, the Fisher and Ford method gave results similar to the Jolly method and would be useful when sample sizes were small; however, it assumes a constant birth rate which may be unrealistic in a field situation. He was concerned that Jolly's method appeared to give standard error estimates correlated with the estimates to which they relate. Manly and Parr's method gave good results when sample sizes were 'moderately large'. Manly's approach is interesting and innovative; regrettably, it does not yield any sort of statistical tool that can be applied to other authors' work.

A different approach was used in the present study. Conceptually, the population 'lives' in an array of numbered sites in the computer. If an animal dies, its site becomes available to another, or new sites are created if needed to house an increasing population. By keeping account of how many sites are in use (even if some are unoccupied), the program (by use of a pseudo-random number generator) ensures that animals are killed at random, and that all live animals have an equal chance of being sampled. Captured animals carry a mark that can be translated to yield their complete trapping history. A facility to allow for the possibility that a sampled animal is killed in handling was included, firstly because this is realistic, and secondly because Jolly's model allows for this contingency. Sample size is not fixed, but varies between limits, which is analogous to the field situation where the size of sample is often dependent on meteorological, human and logistical factors, operating around the biometrician's design of the sampling program.

Other options were built into the program, so that, given a set of field parameters (approximate population size, birth and death rates, etc.), the population could be simulated and various sampling regimes tried out. In addition, the four sub-routines used in the program to estimate popula-

tions can be detached and applied to actual capture-recapture data.

An element of artificiality is produced by carrying through the entire death phase followed by the birth phase. As a result, in growing populations some of the new-born animals are clustered at the upper end of the array. A process to re-randomize the animals in the array prior to sampling was tried, but as this produced no difference in the population estimates (but appreciably increased the amount of computer time used) this was not incorporated in the final model. This may not, in any event, be important: Jolly (1965) points out that the important point is that the probability of capturing a marked animal must be the same as the probability of capturing any member of the population, and this is not changed by the arrangement used.

The eventual aim of this project is to examine different population and sample size combinations, with several birth rate/death rate combinations, to formulate sets of tables to yield more realistic confidence intervals for the models selected.

## POPULATION ESTIMATES

Figs. 1-13, read in conjunction with Table 1, are self-explanatory, and it does not seem necessary to discuss them in detail. Some general conclusions do emerge that are worth amplifying.

1. Bailey's triple catch method never seems to yield particularly satisfactory results. In general, the estimates are not as good as those of the Lincoln index, and this model will be disregarded in the discussion below.

2. Schnabel's method yields excellent results in populations subject to neither birth nor death, or increasing (experiments 1, 4, 6 and, to a lesser extent, the growth phases of other experiments); it will be noted that the standard deviation of the twenty replicates is uniform and reasonably compact (although the standard deviations estimated by the Schnabel model are ludicrously small). This is a most unexpected conclusion as it has always been assumed that recruitment (as well as mortality) would be a source of error (e.g. Ricker 1958, Cormack 1968). Certainly the model, apparently, does not detect mortality: as will be seen in experiments 2 and 3, the model predicts a growing population, while in 5 and 7 it predicts a more or less stable one. Thus if a reliable (preferably independent) estimate of birth and death rates is available, the Schnabel model could provide very good estimates of population size.

3. Lincoln Index and Jolly's estimator generally perform best where the proportion of marked individuals is high (e.g. 5 and 7), in contrast to Schnabel, which performed best where the pro-



portion of marked individuals is low (Fig. 15); an apparent exception is seen in Fig. 1 where prediction by Schnabel was good and the percentage marked was high, but with neither birth nor death the Schnabel model becomes an extended Lincoln estimate. Ricker (1945) claims that the Schnabel estimator has maximum efficiency when a negligible proportion is marked. In this context, note that the Schnabel estimator did not perform as well in experiment 4 as in experiment 6, where the percentage marked was lower (Fig. 15). This is also illustrated in the experiments where the population is declining. For the present regime, where sample size is about 10 per cent or less of the population, there appears to be little to choose between Lincoln Index and Jolly's estimator. However, Jolly's performance is markedly better where birth and death rates are higher—the succession of Lincoln Index estimates show no improvement in performance with time, but the standard deviation for the Jolly estimates is smaller in the last periods than in the first few. (This is most clearly seen in experiment 3.) In addition, the Jolly model provides estimates of birth and death rates (or, more broadly, dilution and loss rates (Southwood 1966)).

4. The variance (or standard deviation) estimates given by the Jolly model are, as Manly (1970) points out, loosely correlated with the estimate to which they apply. This was observed in the present study also, but it is not really surprising. When the true population size is known it is observed that the standard deviation associated with excessively large estimates usually encloses the true population value. In fact, the standard deviations are highly realistic from this point of view, although this would be little consolation to a biologist endeavouring to estimate the population size within a run of several such large estimates of size and standard deviation.

5. It will be observed that the mean of the twenty replicates for all the models follows (with certain exceptions in Schnabel) the true population curve rather well. This suggests that improvements in estimates could be obtained by sub-sampling from populations, where possible, and averaging the estimates rather than relying on point estimates.

Further analyses of the present data are as yet incomplete, for example the relationship between estimates and standard deviations, loss and dilution rates derived by the estimation models. The present study will be broadened by examining the models with different initial population sizes, by using different sampling rates, and by allowing greater variation in sample size, with constant birth and death rates as in experiments 1 to 7.

These should lead to further generalization concerning the validity of the various models.

## CONCLUSIONS

For a series of estimates in a mark-recapture study, Jolly's (1965) model gives the most satisfactory results in situations similar to those tested here, as it includes realistic standard deviation estimates and other data. For the special case of a stable closed population, or one undergoing growth, the Schnabel estimator gives excellent results, although its standard deviation estimate is totally misleading. For those cases where multiple or individual marking of animals is difficult (as in many insects) a series of Lincoln Index estimates gives quite satisfactory results.

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#### DESCRIPTION OF FIGURES 1-16

FIGS. 1-13—These figures summarize the results of experiments 1-13 respectively (see life-history parameters in Table 1). In all cases, the starting value for the population was 1000; sample size was  $100 \pm 10$ ; and the probability of loss during handling was 3%.

The upper half of each figure shows the actual estimates obtained in periods 2-9 in two replicates selected randomly, using (left to right) the Lincoln, Schnabel, Bailey and Jolly models. Where estimates exceed the limits of the scale (shown on the right) the estimate is shown in numbers.

The lower half of each figure (left hand scale) shows the mean (horizontal bar)  $\pm 1$  standard deviation (vertical bar) over the twenty replicates, using the same models.

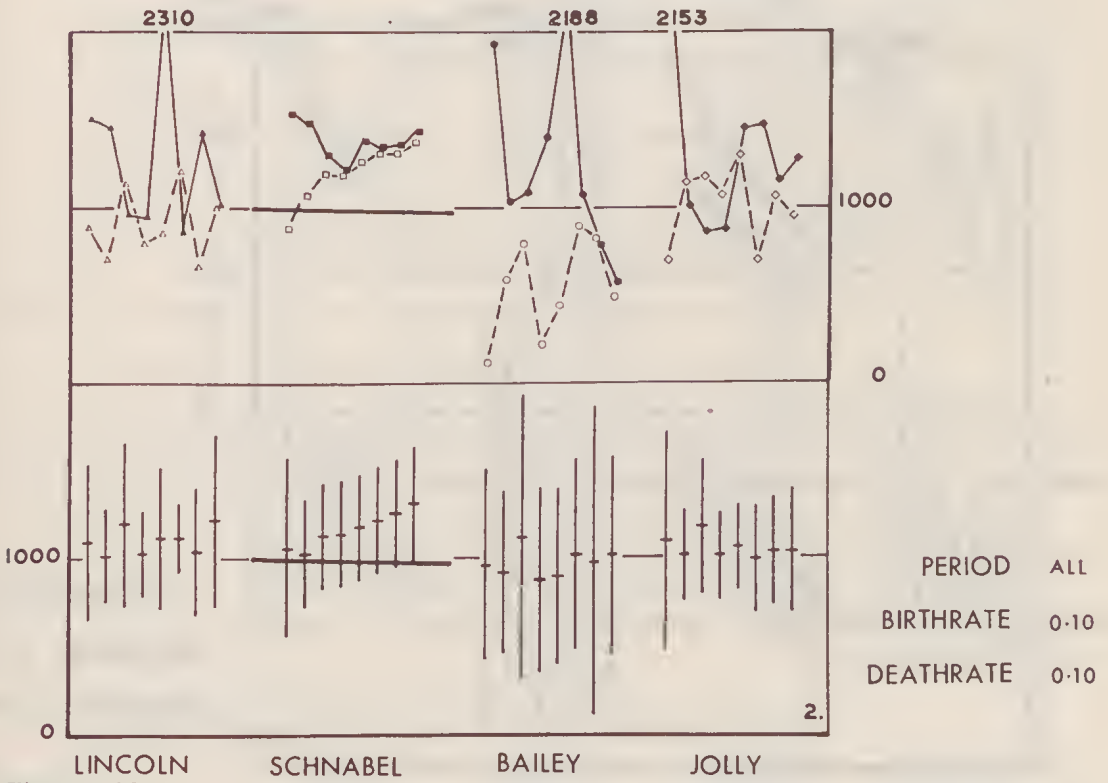
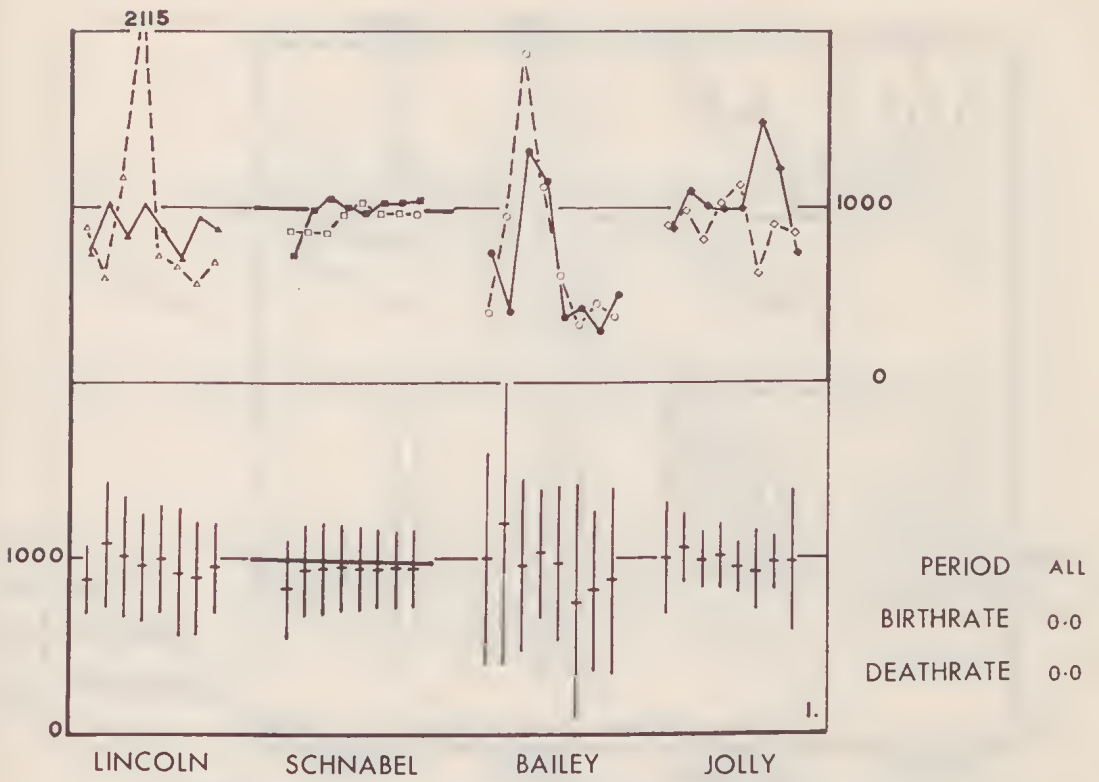
The solid line shows the actual population trend.

FIG. 14—Distribution of estimates by Jolly model for births = deaths = 0. Each point represents an estimate in the appropriate period, the horizontal bar the mean, and the vertical bar  $\pm 1$  standard deviation.

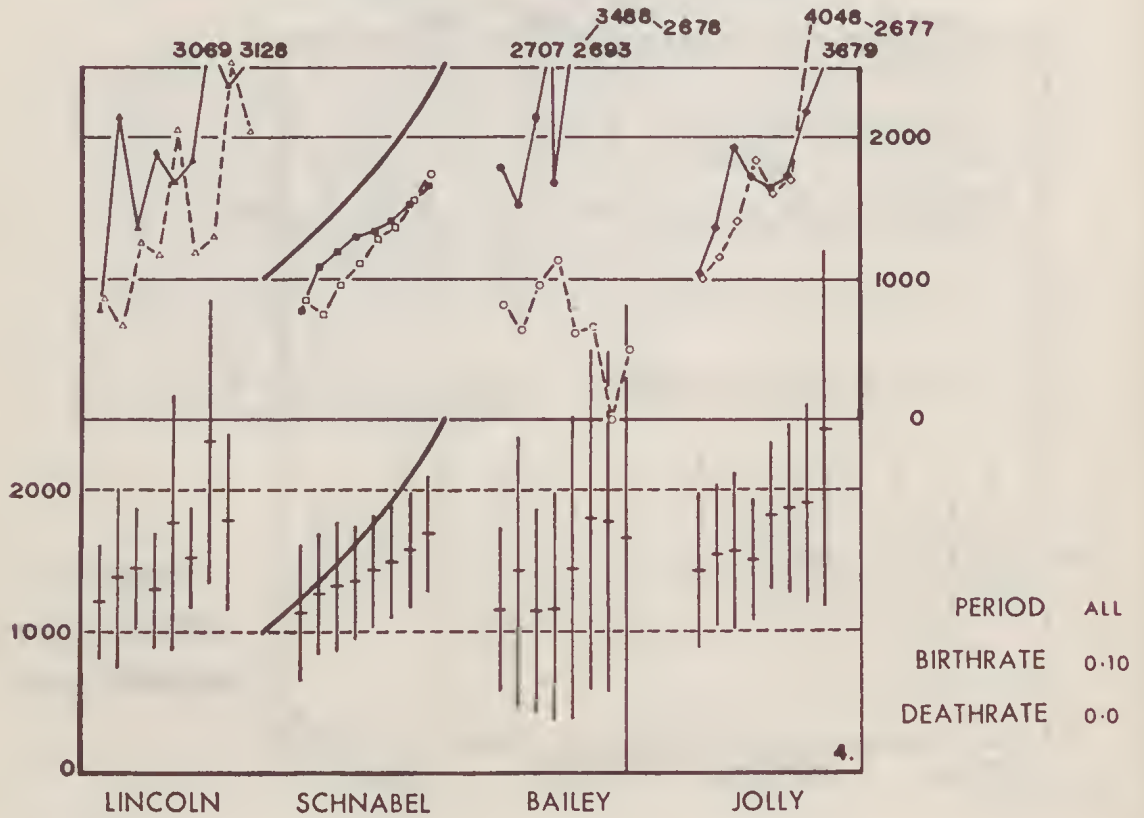
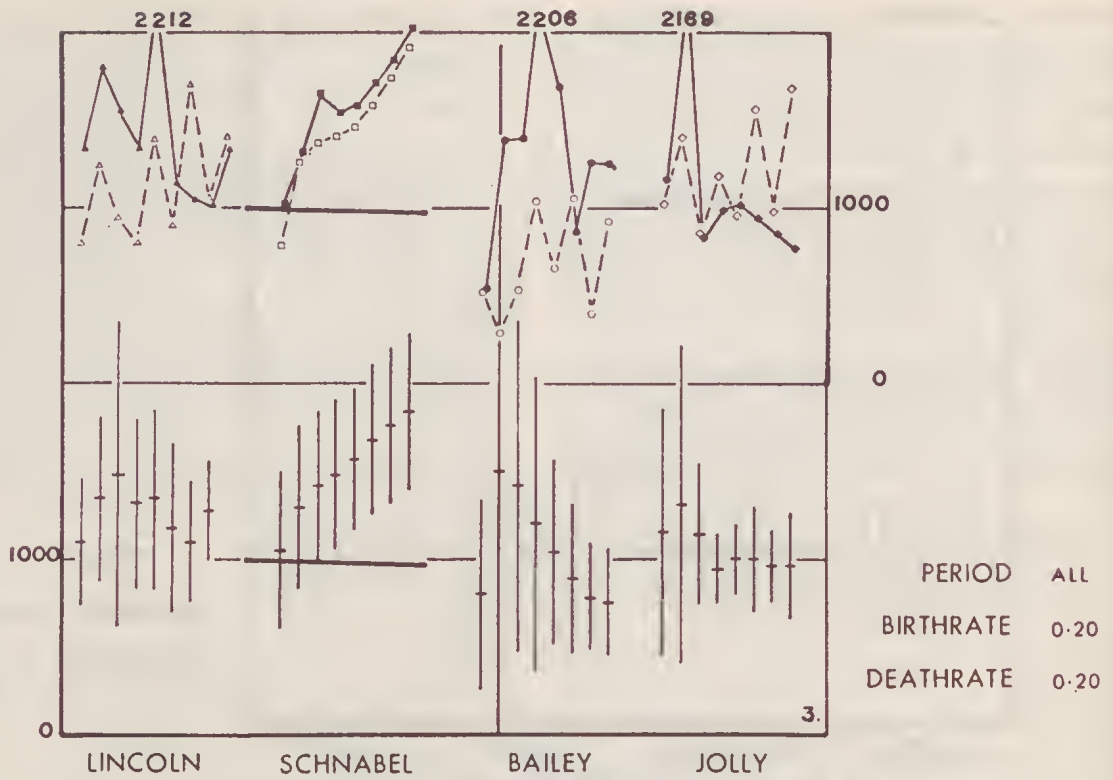
FIG. 15—Percentage of marked individuals, by time periods, for each of the experiments 1-13.

FIG. 16—Flow diagram of main program.



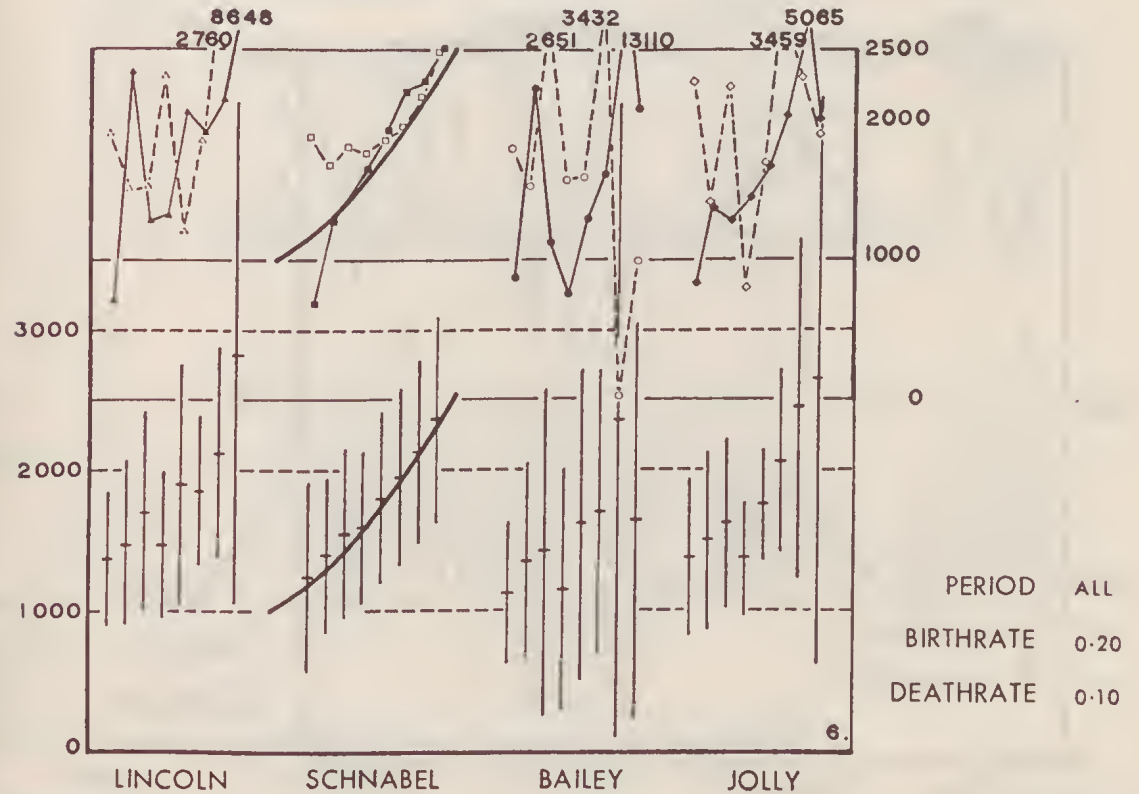
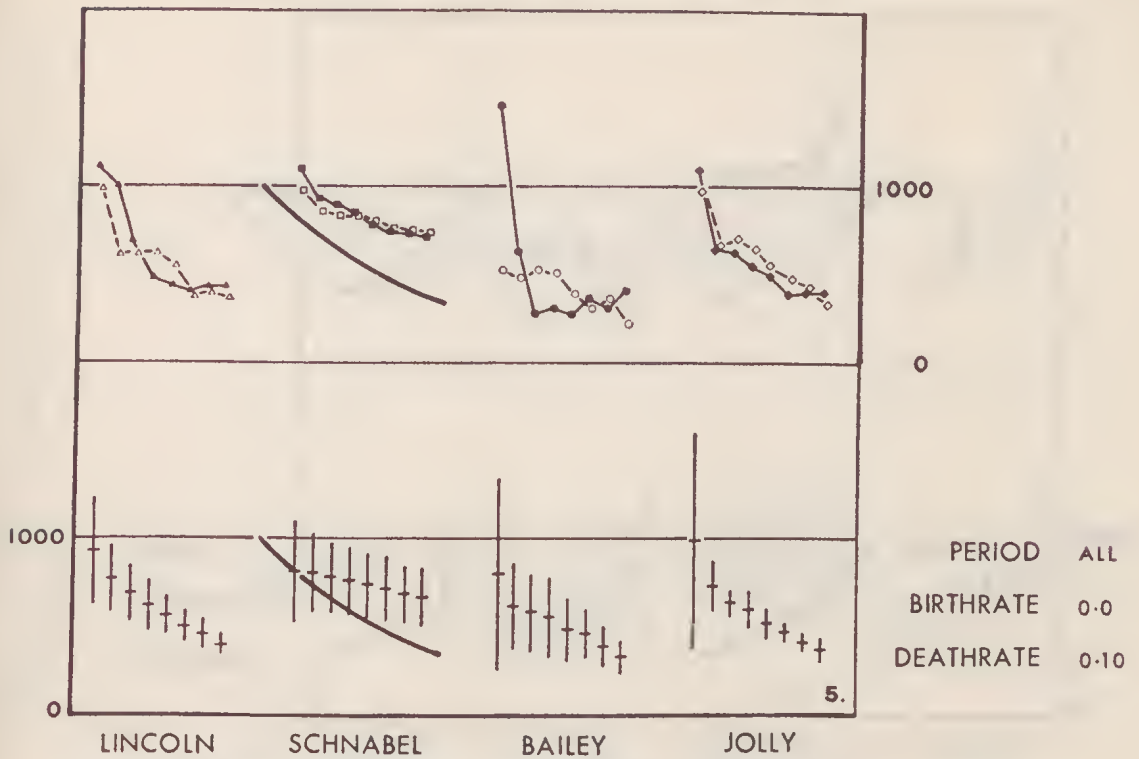


Figs. 1 and 2

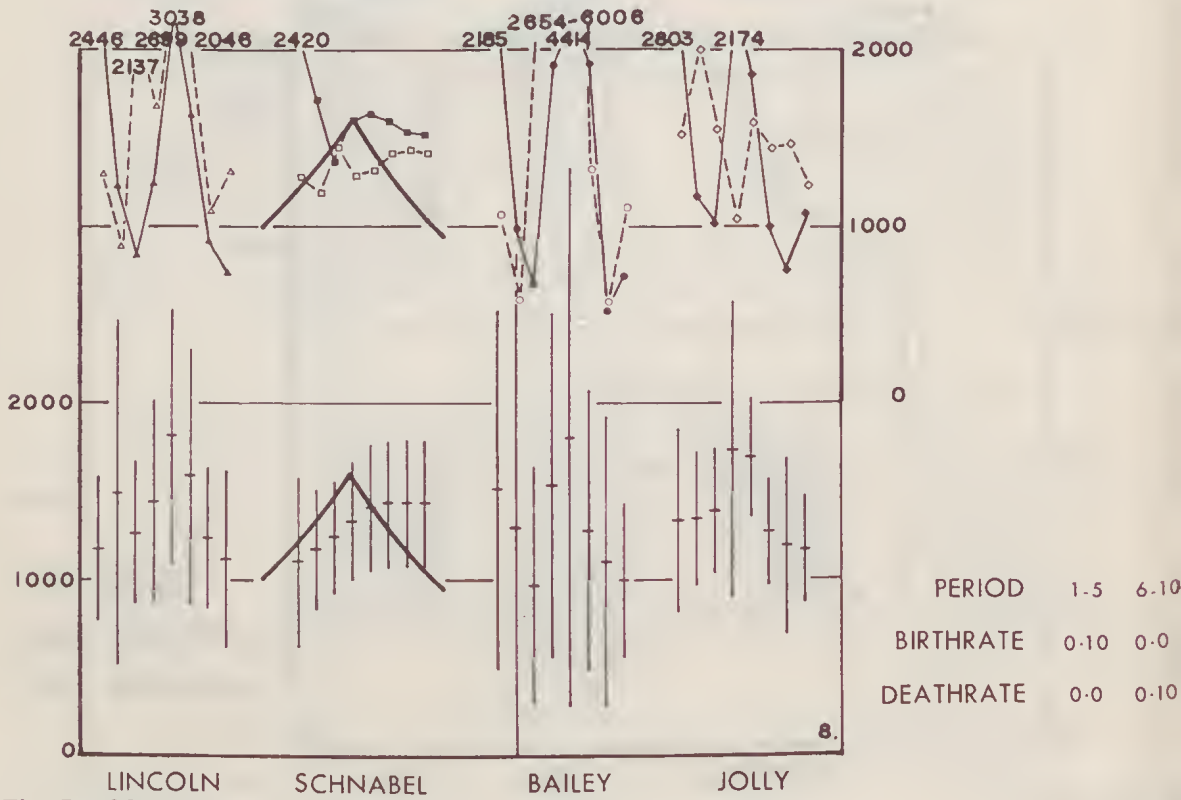
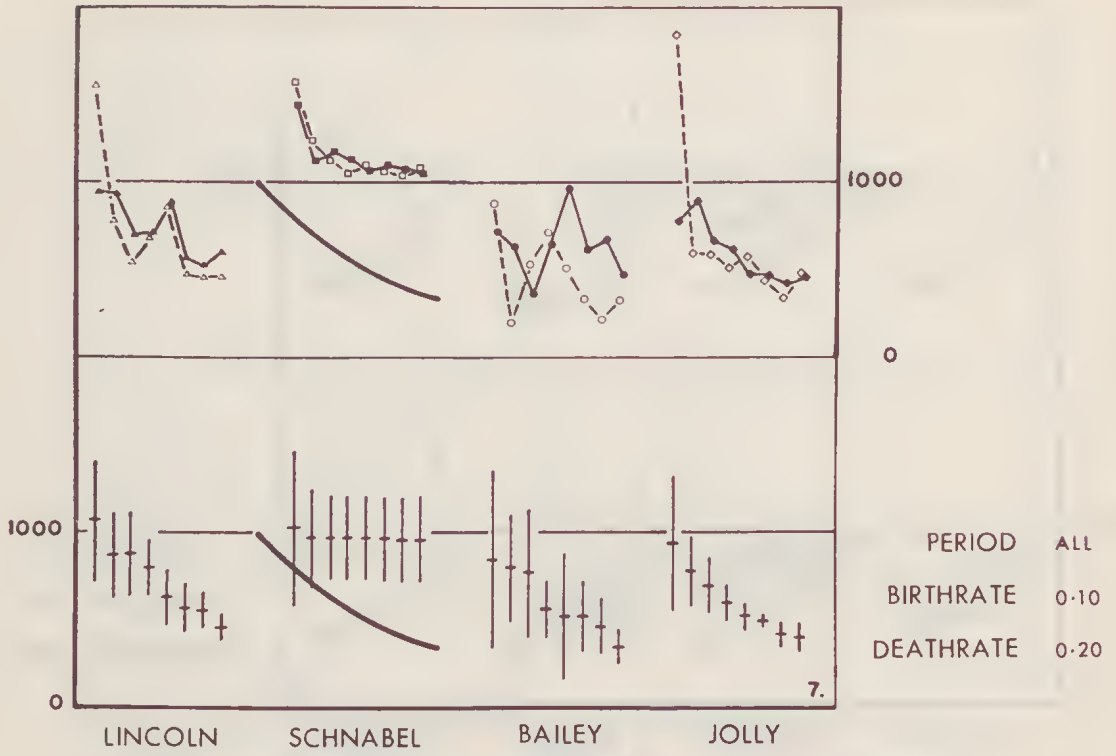


Figs. 3 and 4

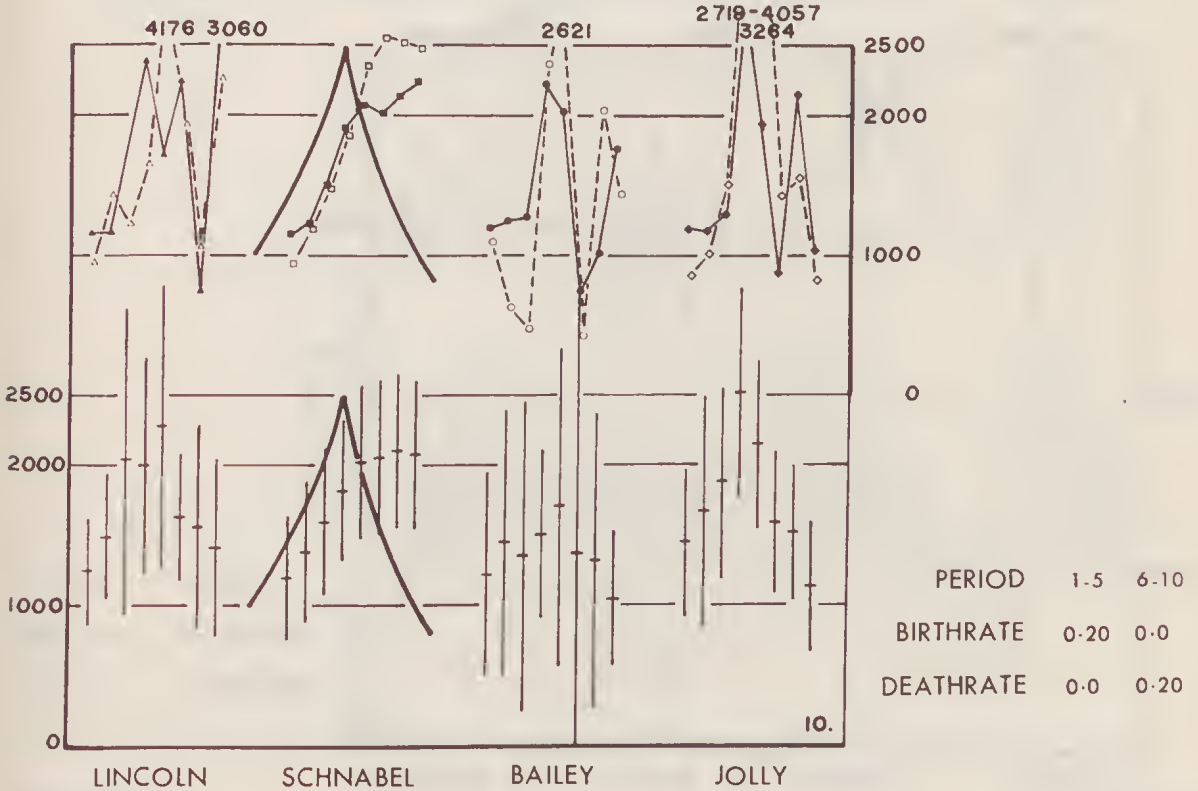
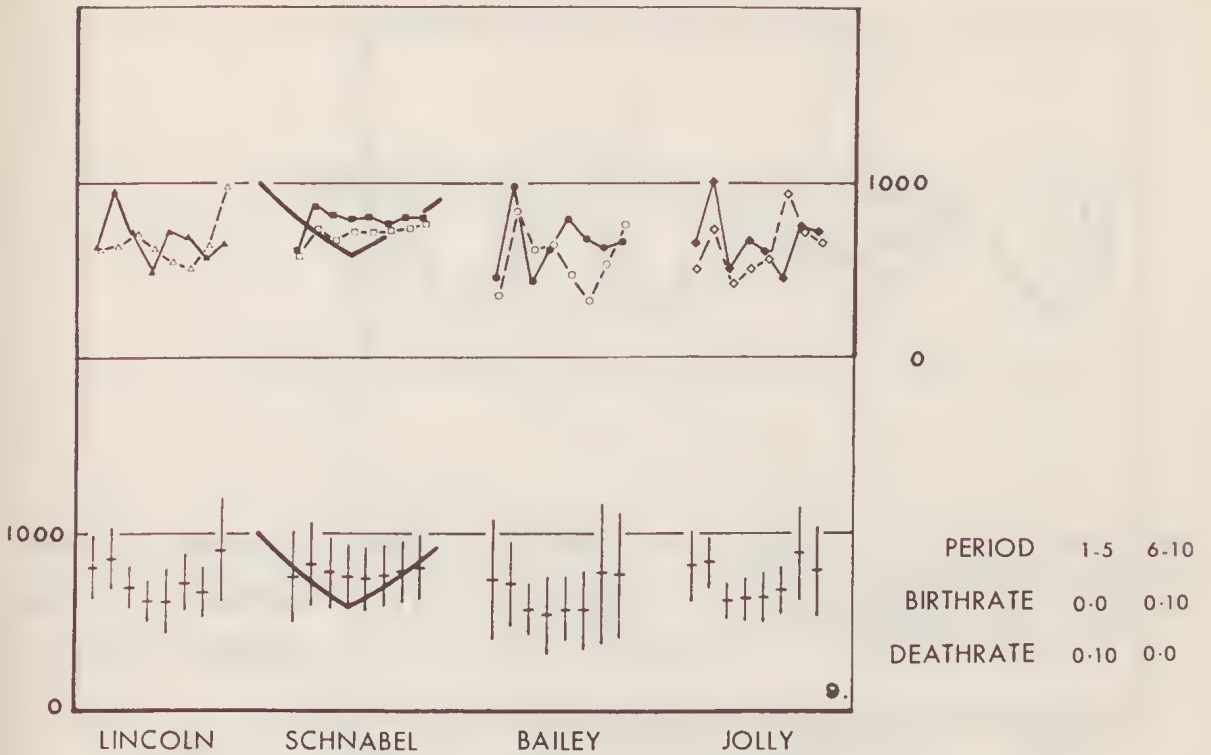




Figs. 5 and 6

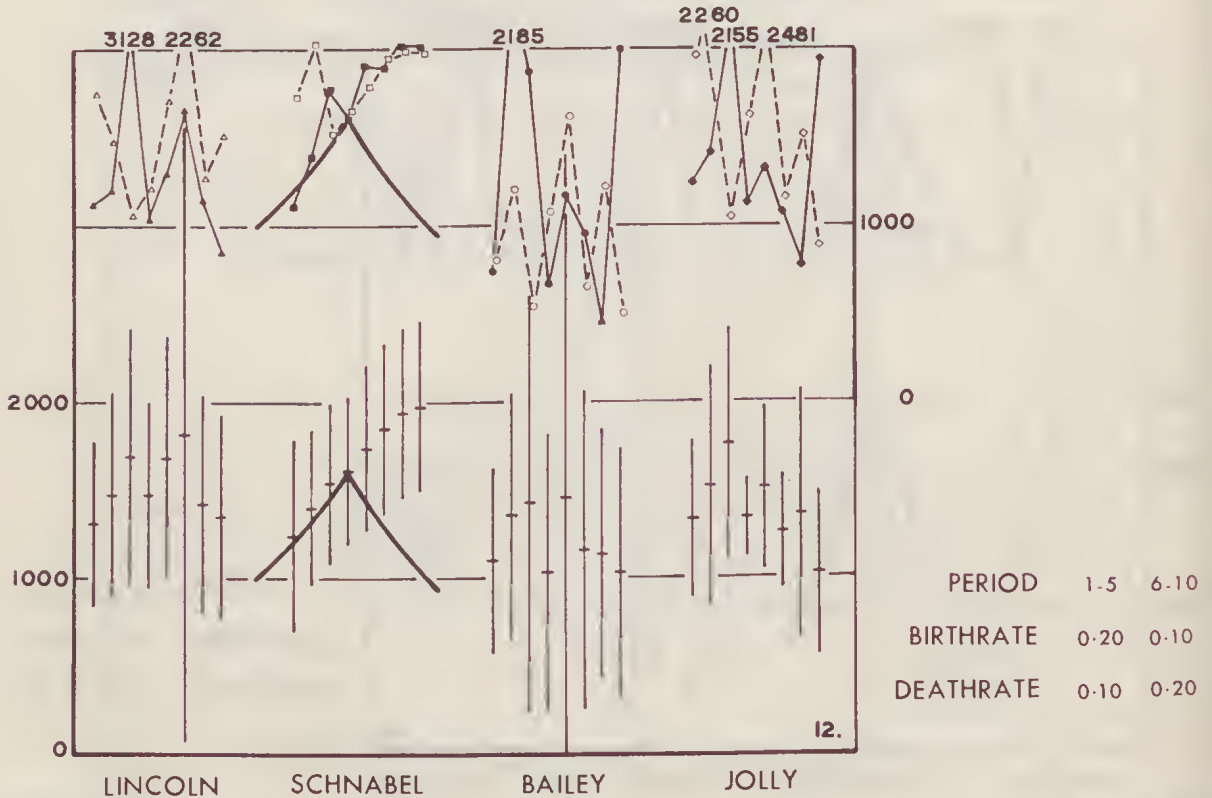
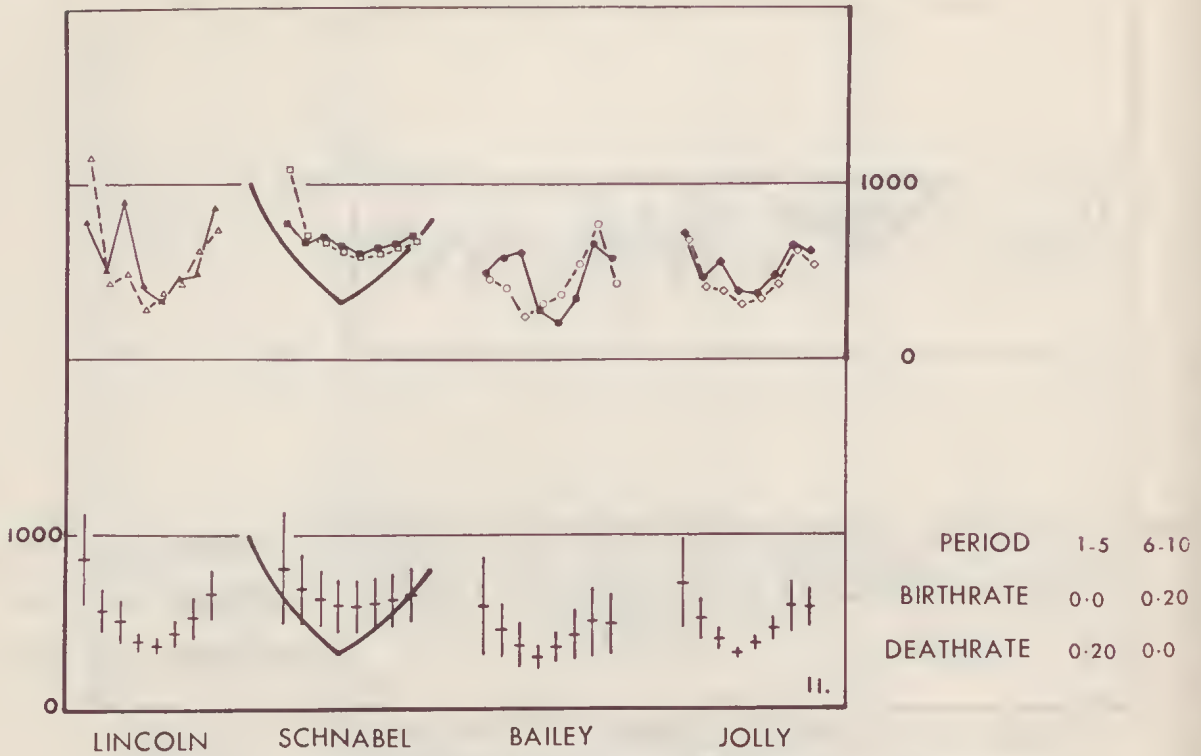


Figs. 7 and 8

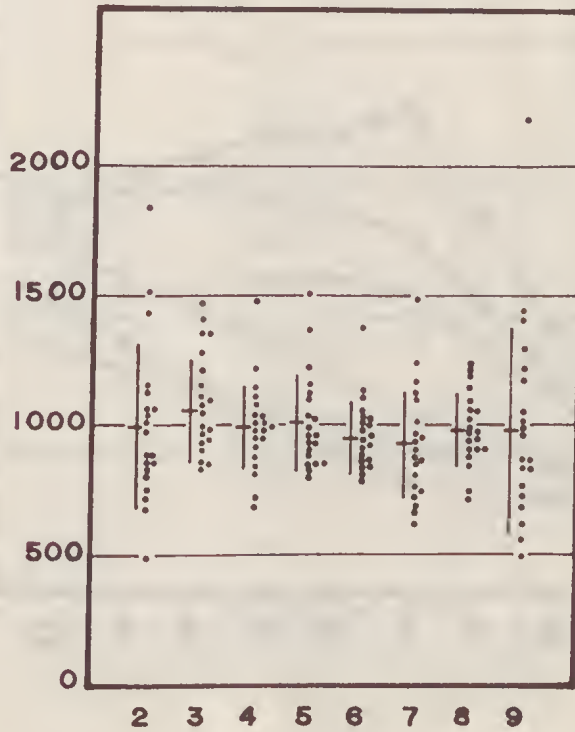
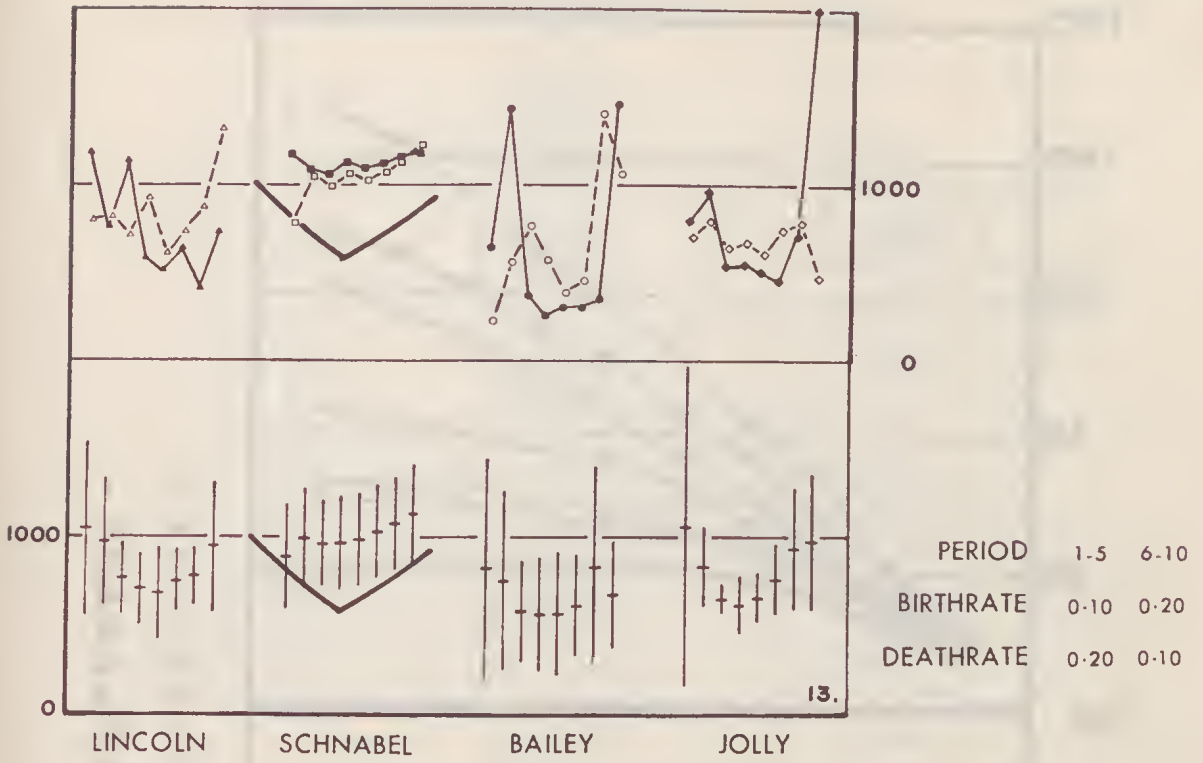


Figs. 9 and 10





Figs. 11 and 12



Figs. 13 and 14

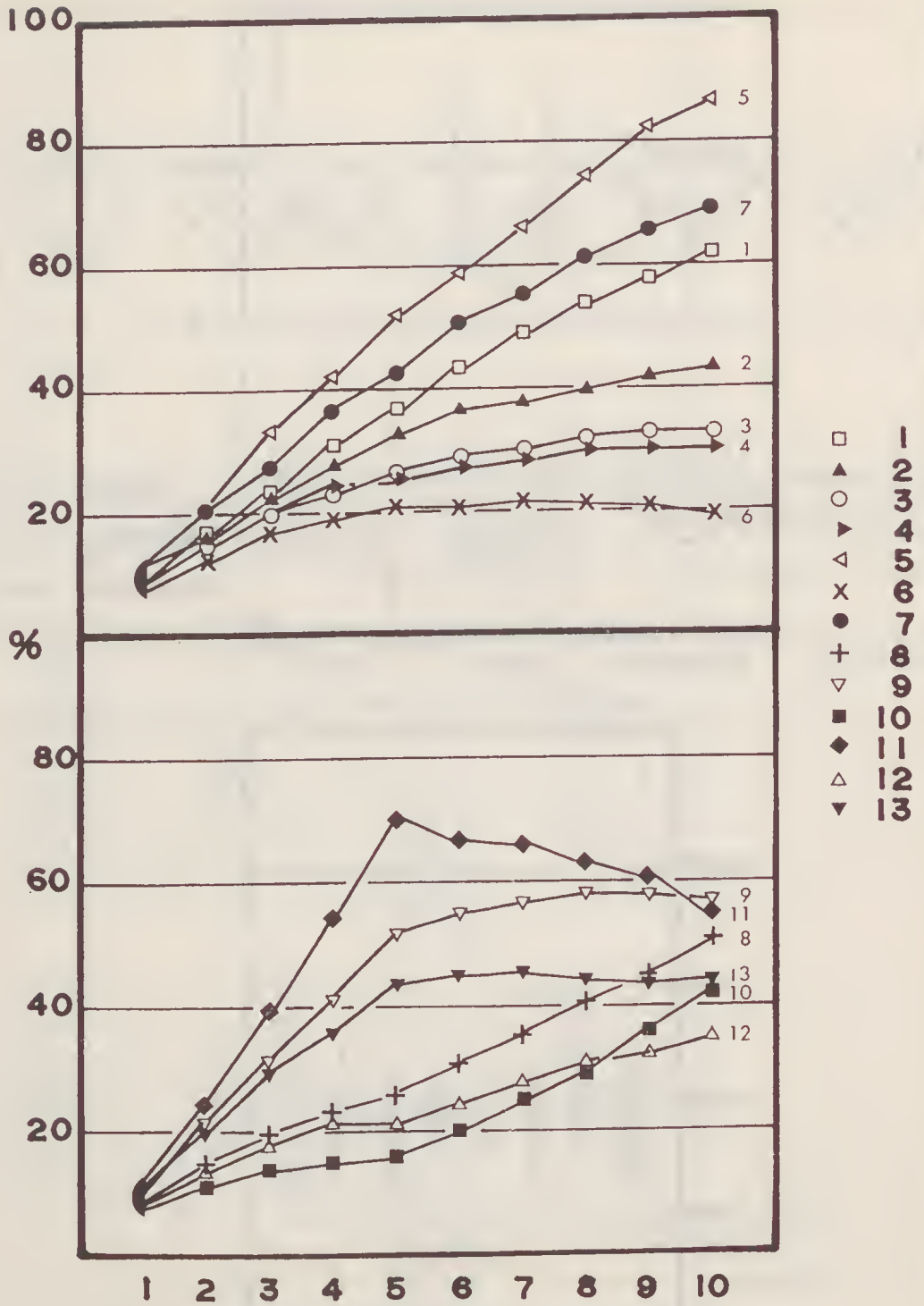


Fig. 15



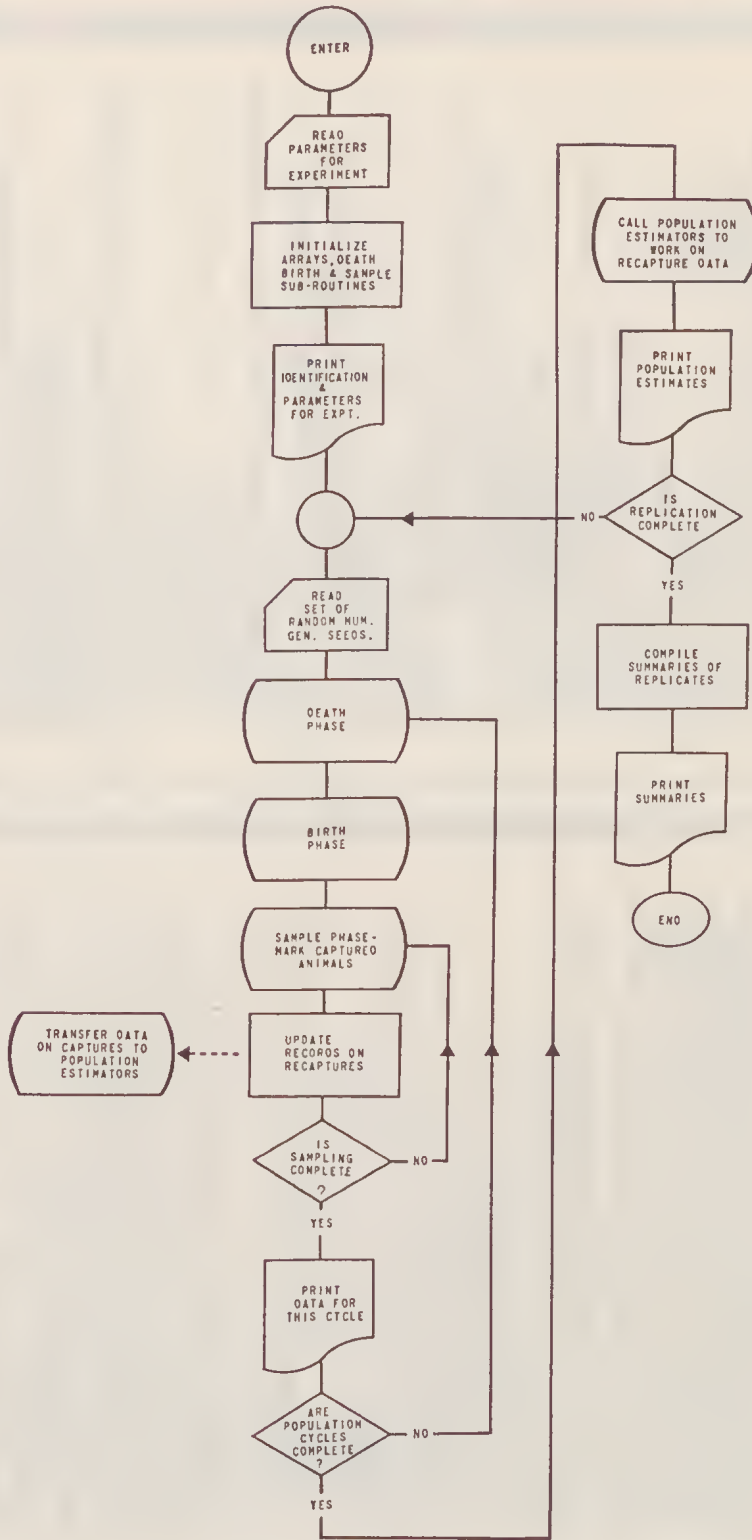


Fig. 16

APPENDIX
FORTRAN 4 LISTING OF PROGRAM 'SYNPOP'

\*\*\* PROGRAM SYNPOP \*\*\*
VERSION DATED JULY 1973
THE PROGRAM SYNPOP IS INTENDED TO SIMULATE AN IDEALIZED
NATURAL POPULATION OF ANIMALS, THE SIZE OF WHICH IS TO BE ESTIMATED BY A MARK-RECAPTURE METHOD, STARTING FROM AN INITIAL SET OF THE POPULATION. INDIVIDUALS ARE MARKED AND RELEASED, AND AS THEY RECAPTURE, INDIVIDUALS ARE MARKED AND RELEASED. AN OPTION ALLOWS SOME TO BE KILLED IN HANDLING - THEIR RECORDS ARE SEPARATED FROM THE OTHERS, AS ARE THOSE OF MARKED ANIMALS KILLED IN THE WILD. THE EXPERIMENTER SPECIFICS EITHER FIXED BIRTH AND DEATH RATES, OR STOCHASTIC DRIFTS, AND MAY SPECIFY LIMITS. HE MAY ALSO SPECIFY WHETHER BIRTHS ARE TO EXCEED DEATHS OR VICE VERSA. THESE OPTIONS ARE EXPLAINED BELOW, ON THE PARAMETER CARDS.
THE RECORDS OF MARKED ANIMALS KILLED IN THE WILD ARE STORED IN ARRAY MUKILL, THOSE KILLED BY HANDLING ARE IN ARRAY SMLIND AND THE REST OF THE POPULATION IS IN ARRAY POP.
SHRINKING IS REQUIRED
SAMPLE (WITH SUB-ENTRY SAMPLE2)
DEATH (WITH SUB-ENTRY DEATH2)
BIRTH (WITH SUB-ENTRY BIRTH 2)
LINC (LINCOLN INDEX ESTIMATOR)
SCHWARZ (SCHWARZ ESTIMATOR)
BALLEE (BALLEE TRIPLE-CATCH ESTIMATOR)
JULLIEN (JULLIEN STOCHESTIC ESTIMATOR)
LINCSP
LINCSPH
OALSUM
JOLSUM
PRINT
TRIVAL
FUNCTION RNDM (RANDOM NUMBER GENERATOR)
DATA DECK STRUCTURE
THE FIRST CARD GIVES INFORMATION ABOUT THE EXPERIMENT (ALPHANUMERIC IN COLUMNS 1-20), AND THE NUMBER OF SETS OF PARAMETER CARDS TO FOLLOW (COLUMNS 21-22).
THE NEXT CARD HAS AN UND INTEGER NUMBER IN 110 ENRMAT TO SFFO
THE MACHINE-INTRINSIC RANDOM NUMBER GENERATOR
\*\*\*\*\* NOTE THAT THIS PROCEDURE DIFFERS SLIGHTLY FROM THAT DESCRIBED IN THE TEXT ABOVE \*\*\*\*\*
THE FOLLOWING PARAMETERS ARE USED
1. SAMPLE SPECIFICATION CARD
2. BIRTH CARD
3. DEATH CARD
I. SAMPLE SPECIFICATION CARD
COL. INFORMATION (CALL MUST BE RIGHT JUSTIFIED)
I=6 SFFO VALUE FOR POPULATION
7=8 NUMBER OF SAMPLING CYCLES REQUIRED
10 BIRTH/DEATH OPTION 0 = FLOAT WITHIN SPECIFIED BIRTH/DEATH OPTION 1 = LIMITS OFFAULT VALUE)
FUH STOCHASTIC RATES 1 = BIRTHS,GE=DEATHS
2 = BIRTHS,GE=DEATHS





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56 WPIF(LL,35) DENOAY,OFPIE
57 GOTO 60
58 WRITE(4,37)
59 CONTINUE
C
C
C GET INITIAL POPULATION ROMN
UC NO I=1,SEED
RO POP(I)=99
C
C
C COMMENCE POPULATION CYCLES
C
C
C DO 400 KK=1,NCYCL
CHECK IF POPULATION WITHIN BOUNDS = IE NOT, INCRFASZ BOUND
IF(POP(SIZ+GT,MAXPOP) MAXPOP=POP(SIZ
ZFRD COUNTFNS
95 NKKLU=0
NPEL=0
ICAP=0
KMARK=0
NOEAD=0
MKSAB=0
LJNCK=0
NS=0
KT=0
POPNUM=POPSIZ
MAXPUP=MAXPUP
PREPARE ALL PREVIOUSLY MARKED ANIMALS TO RECEIVE A NEW MARK
IF(KK=0) GOTO 397
DO 100 J=1,MAXPOP
JOP(J)=0
IF(JUE=NC,99,AND,JUE,NE,0) POP(J)=POP(J)+10
385 CONTINUE
397 CONTINUE
C
C
C OBTAIN NUMBER OF DEATHS FOR THIS CYCLE
I NCYCL,IG,8910)
OBTAIN NUMBER OF BIRTHS FOR THIS PERIOD
CALL BIRTH(KK,POPSIZ,NOVOTH,LIMO,PROTH,DTMHTF,NOFU,OF,UGAY,OFRTF)
1 RITE=NCYCL,IRD,I,4,8920)
KILL OFF PREVIOUSLY MARKED ANIMALS
C
C
IF(NMOTH=GT,POPSIZ) GOTO 950
IF(NMOTH=EQ,0) GOTO 175
DO 170 I=1,NMOTH
NM=IFIX(RNUM(I)*MAXPOP+0.5)
IF(NM=GT,MAXPUP) NM=MAXPUP
IF(NM=LT,1) NM=1
CHECK IF ANIMAL ALREADY DEAFU
IF(POP(NM))100,100,140
CHECK IF ANIMAL UNMARKED = IF SO KILL HIM
140 IF(POP(NM)=99)150,150,160,150
IF ANIMAL ALREADY MARKED, KEEP HIS RECORD IN "BLOCK II" AND TRFII
C
C
150 KTKT=1
ALUKIL(KT)=POP(NM)
160 POP(NM)=0
NOEAD=NOEAD+1
POPSIZ=POPSIZ-1
170 CONTINUE

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175 #POP(I)=POPSIZ
C
C ENTER BIRTH CYCLE
NNMTH=NUMBTH
IF(NMOTH,Eq,U)GOTO 270
DO 200 J=1,MAXPUP
IF(POP(J)) 200,180,200
180 POP(J)=99
POPSIZ=POPSIZ+1
IF(NMOTH,Eq,1) GOTO 270
NMNTH=NUMBTH-I
200 CONTINUE
MX=MAXPOP+1
MAXPOP=MAXPOP+NMNTH
UO 260 J=MX,MAXPUP
POP(J)=99
POPSIZ=POPSIZ+1
260 CONTINUE
270 CONTINUE
NNNSPL=POPSIZ
IRUPUP(KK)=POPSIZ
C
C URAM SAMPLES
CALL SAMPLECOUN,POPSIZ,NSAMPL,LIHT,PERSPL,VAR,IS,8900)
IF(NM,LT,POPSIZ)GOTO 270
WRITE(4,962) NM,POPSIZ
NM=POPSIZ
280 DO 340 J=1,NM
SELECT LIVE ANIMAL
290 NM=IFIX(RNUM(I)*MAXPOP+0.5)
IF(NM,GT,MAXPOP)NM=MAXPOP
IF(NM,LT,1)NM=1
CHECK IF THIS ANIMAL IS OFAD (=0) = IF SO, GET ANOTHER ANIMAL
320 IF(POP(NM))290,290,330
CHECK IF PREVIOUSLY MARKED
330 IF(POP(NM)=99)340,335,340
ANIMAL NOT MARKED
335 POP(NM)=1
ICAP=ICAP+1
GOTO 355
C
C ANIMAL CARRIES A MARK
C
C
IFST IF ANIMAL MARKED ALREADY IN THIS CYCLE
340 MARK=POP(NM)
MARK=MARK+(MARK/10)*10)
IF SO RETURN AND SELECT ANOTHER BEAST
IF(MARK-1)345,290,345
IF NOT,CALL POPULATION COUNTERS
345 IF(CK,EG,1) GOTO 350
JCK=POP(NM)
IF(CJK,10=(JCK/100)*10),EG,1) LJNCK=LJNCK+1
MKSAB=MKSAB+1
MARK(MKSAB)=JCK/10
CALL JOLLIT(KK,JCK)
CALL HALL(KK,JCK)
CALL HARK IT
INDU HARK IT
350 POP(NM)=POP(NM)+1
ICAP=ICAP+1
355 NREL=NREL+1
CHECK IF ANIMAL KILLED IN MARKING
IF(ICR)360,360,360

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360 CONTINUE
PROGRAMM(ITT)
IF(POP0-PRJ370,370,360)
TRANSFER RECORD OF MARKFD ANIMAL TO ARRAY *SNPLOD*
370 KS=KS+1
SNPLOC(KS)=POP(NUM)
POP(NUM)=0
POPSIZ=POPSIZ+1
NREL=NREL+1
380 CONTINUE
WRITE(1P,39)IFLAG
IFLAG=IFLAG+1
C
CALL SCHNAB(KK,AKSNAB,NCAP,NREL,NREPS,NRP)
C
C GATHER UP DATA FOR THIS CYCLE
TOTCAP(KK)=NCAP
TOTREL(KK)=NREL
SCAP(KK)=TOTCAP(NCAP)
SREL(KK)=TOTREL(NREL)
TOTR(KK)=ELNCHK
C
C PRINT OUT RESULTS FOR THIS CYCLE
IF(MR+EG,0)GOTO 415
WRITE(1P,4)KK
WRITE(1P,5)POPNUM,MAXPOP,NOFAD,NPOPC,NNNBTH,NNNSPL
WRITE(1P,6)NKKN,NCAP,NREL,KS,KT
IF(AKSNAB)AD5,AD5,402
402 WRITE(1P,11)
WRITE(1P,8)(M,ARX(K),K=1,M,AKSNAB)
405 IF(KS) 410,410,407
407 WRITE(1P,7)
WRITE(1P,8)(SMPLD(K),K=1,KS)
410 IF(KT) 418,418,415
415 WRITE(1P,9)
WRITE(1P,8)(ALDKIL(K),K=1,KT)
418 IF(MPR,EG,0)GOTO 420
WRITE(1P,10)
WRITE(1P,8)(POP(K),K=1,MAXPOP)
420 KCYCL=KK
C
KOUNT=0
DO 500 I=1,MAXPOP
MARK=POP(I)
IF(MARK,EG,99) KUUNT=KOUNT+1
500 CONTINUE
NKKANL=POPSIZ-KOUNT
A=NKANL
B=POPSIZ
MFKMS=I/R,100,0
WRITE(1P,510)KUUNT,NKKANL,PERMKS
400 CONTINUE
C
CALL LINC(KCYCL,TOTCAP,TOTREL,TOTMK,NREPS,NRP)
CALL SNABPR(KCYCL,NRP,NREPS)
CALL BIL2(KCYCL,NRP,NREPS)
CALL JOL2(KCYCL,NRP,NREPS)
CALL TRUVAL(KCYCL,NRP)
IF(NAP,EG,NREPS)CALL TRUPR(KCYCL,NREPS)
GOTO 1000
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C
C DIAGNOSTIC PRINTOUT
900 WRITE(LP,902)
GOTO 1000
910 WRITE(LP,912)
GOTO 1000
920 WRITE(LP,922)
GOTO 1000
930 WRITE(LP,932) IRD,BTRHTF,DTHRTE,MH8TH,PROTH
GOTO 1000
950 WRITE(LP,952) NMHOTH,POPSIZ
1000 CONTINUE
C
STOP
END
SUBROUTINE DEATH (L,NUMPOP,NUMHOTH,L1HD,P,DR,N,TOAYS,RATE,NC,IX,*)
DIMENSION IWAYS(20),HATF(20)
NEN=+1
GOTO(10,30,20,40),NN
10 NMHOTH=0
HFTURN
20 IF(PR,EG,0,0) RFTURN 1
LTM=FIX(NUMPOP*PR+0.5)
PREP=RRNUM(IX)
NMHOTH=FIX(NUMPOP*PR+0.5)
HFTURN
30 IF(DM+EO,0,0)RETURN 1
NMHOTH=FIX(NUMPOP*OR+0.5)
HFTURN
40 DO 60 I=1,NC
IF(L-IWAYS(I))60,50,60
50 SOR=HATF(I)
IF(RATE(I),EG,0)SOR=DR
60 CONTINUE
HNMOTH=0
HFTURN
70 NMHOTH=FIX(NUMPOP*SOR+0.5)
HFTURN
END
SUBROUTINE BIRTH (L,NUMPOP,NUMDEP,NUMBTH,LDTH,P,DR,N,TOAYS,RATF,BC
1,LDTH,IX,*)
DIMENSION IWAYS(20),HATF(20)
PREP
NM=+1
GOTO(10,50,20,60),NN
10 NMHOTH=0
HFTURN
20 IF(PR+EO,0,0)RETURN 1
LR=FIX(NUMPOP*PR+0.5)
PREP=RRNUM(IX)
NMHOTH=FIX(LRMPOP*PR+0.5)
190A=180+1
GOTO(100,30,35),180A
30 IF(NMHTH,6E,NUMDEP) RETURN
GOTO 40
35 IF(NMDFD,6E,NUMBTH)RETURN
40 IFNP=NUMBTH

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A11 C IF(NRP.FG.I)CALL SNBSUN(NRPS,AK)
A12 C IF (K=1)IO=10,30
A13 C IO 20 I=1,20
A14 C IO 15 J=1,9
A15 C I5 NAB(I,J)=0
A16 C IO 20 J=1,4
A17 C 20 ANS(I,J)=0,0
A18 C NAB(I,J)=K
A19 C NAB(I,2)=NCAP
A20 C NAB(I,3)=HREL
A21 C NAB(K,1)=K
A22 C NAB(K,2)=NCAP
A23 C NAB(K,3)=HREL
A24 C NAB(K,4)=NAB(K-1,4)+NAB(K-1,3)-NAB(K-1,6)
A25 C NAB(K,5)=NAB(K-1,5)+NAB(K-1,2)+NAB(K-1,4)
A26 C NAB(K,6)=NAB(K-1,6)
A27 C NAB(K,7)=NAB(K-1,7)+NAB(K-1,5)
A28 C NAB(K,8)=NAB(K,5)/(NAB(K,7)+1)
A29 C ANS(K,5)
A30 C IF(A=0)O=0,100 IN 50
A31 C ANS(K,1)=SQRT((C=C/A)*(1+C*2,0/A))
A32 C ANS(K,2)=(NAB(K,8)-TRUPOP(K))/TRUPOP(K)
A33 C CALL SUKSNB(K,C,AR,NCYCL)
A34 C 50 RETURN
A35 C
A36 C ENTRY SNARPR(NR,NRP,NRPS)
A37 C WRITE(1,1)
A38 C IO 60 I=1,N
A39 C WRITE(1,2)NAB(I,J),J=1,4,NAB(I,6),NAB(I,8),ANS(I,1),ANS(I,2)
A40 C CONTINUE
A41 C 1 FORMAT(1H0,///20X,"POPULATION ESTIMATES - SCHNABFL POOLICATION",
A42 C 2"PERIOD NUM, //20X," O. LINCOLN IMPR",//20X, "BIAS",//
A43 C 3 20X, CAPT. RELO. RCAPS MARKS POPLN "/)
A44 C IF(NRPT.NRP)STOP
A45 C CALL SNBTIT(NRPS)
A46 C CALL PRINT(NRP,NRPS,K,42)
A47 C RETURN
A48 C
A49 C SURROUTINE BAILY(NRP,NRPS)
A50 C *****
A51 C SURROUTINE BAILY ESTIMATES ANIMAL POPULATION SIZE FROM MARK
A52 C RECAPTURE DATA BY BAILY'S TRIPLE-CATCH METHOD.
A53 C
A54 C REF. BAILY, N-J, 1947. IMPROVEMENTS IN THE INTERPRETATION OF
A55 C RECAPTURE DATA. J. ANIM. ECOL. 21, 120-7
A56 C
A57 C USE = CALL BAILY(NR)
A58 C CALL BAILY(K,NUM)
A59 C CALL BAILY
A60 C COMMON TC,TR
A61 C WHERE ND = NUMBER OF TRAPPING DAYS
A62 C K = ORDER NUMBER OF ANY TRAPPING DAY
A63 C NUM = MARK CODE OF AN ANIMAL, IN THE FORM 11010,
A64 C
A65 C
A66 C
A67 C
A68 C
A69 C
A70 C
A71 C
A72 C
A73 C
A74 C
A75 C
A76 C
A77 C
A78 C
A79 C
A80 C
A81 C
A82 C
A83 C
A84 C
A85 C
A86 C
A87 C
A88 C
A89 C
A90 C
A91 C
A92 C
A93 C
A94 C
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A96 C
A97 C
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A99 C
700 C
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731 C
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C *****
C SURROUTINE BAILY(NRP,NRPS)
C
C TC = VECTOR OF TOTAL CAPTURES ON EACH DAY
C TR = VECTOR OF TOTAL RELEASES ON EACH DAY
C *****
C SURROUTINES NEEDED = NONE
C *****
C DIMENSION TC(20),TR(20),DC(20,20),TRUPOP(20),AR(20,2)
C REAL NZ,NZ3
C COMMON TC,TR,TRUPOP /COMMON/AR,DC
C COMMON JP
C IF(C=NR.FG.I)CALL BALSUP(AR,NRPS)
C IO 5 I=1,20
C IO 5 J=1,20
C UC(I,J)=0,0
C 5 CONTINUE
C
C 10 FORMAT("0",///5X,"RAW DATA = COLS AND NO. CAPTURED, NO. RELEASED,
C 1 AND NO. OF MARKS CAPTURED EACH DAY",//)
C 20 FORMAT(1H0,12F8,0)
C 25 FORMAT("0",20X)
C 3"PERIOD EST. LOSS
C 3" POPLN FREQ RATE
C 3" POPULATION ESTIMATE BY BAILY "BIAS",//
C 1 FORMAT(1H1,20X,"TRIPLE-CATCH METHOD")
C 40 FORMAT(20X,14,7Y,F6,0,3X,F9,3,1X,F8,3,4X,F8,3,2X,F8,4)
C RETURN
C
C ENTRY BAILY(K,NUM)
C N=NUM/10
C K=K-I
C IO 45 J=1,K
C L=K-J
C N=N-(C/10)+10)
C IF(N=0) UC(K,L)=DC(K,L)+I
C N=N/10
C 45 CONTINUE
C RETURN
C
C ENTRY BAILY(NR,NRPS)
C WRITE OUT ANWAY OF RAW DATA
C WRITE(1,30)
C WRITE(1,10)
C WRITE(1,20)TC(I),TR(I),J=1,11)
C WRITE OUT RESULT TITLE
C CALCULATE AND WRITE OUT RESULTS
C N=0 I=2,NC
C F=0,0
C N=NR=0,0
C D=TR=0,0
C A=TR(I-1)
C A=TR(I)
C N=TC(I)+I
C N=TC(I+1)+1

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      KPI=0C(I,I-1)+1
      KPI=0C(I+1,I-1)
      N3=0C(I+1,I-1)+1
      IF(R21+R31+R32+R2+R0+R1+R0
84 P=AZ+R2+R31/(R21+R32)
      SF=SORT(P,P) -(A2+R2+R2+R31*(R31+1)/(R21+R21+1)+R32*
      1(R32+1))
      GAMMA=ALOG(A2+R31/(A1+R32))
      GAMMA=-GAMMA
      DFTATEXP(R21+R31/(R2+R31))
      BIAS=(P-TRUPUP(I))/TRUPUP(I)
C
88 WRITE(LP,40) I,P,SE,GAMMA,BFJA,R1AS
      CALL BIAS(P,L,AR)
90 CONTINUE
      IF(NP=1)NRP=RETURN
      CALL BIAS(NRPS)
      CALL PRINT(NRP,NRPS,L,AR)
      RETURN
      END
C*****
C SUBROUTINE JOLLY (NRP,NRPS)
C *****
C SUBROUTINE JOLLY
C USES THE STOCHASTIC METHOD OF C. W. JOLLY TO OBTAIN
C POPULATION ESTIMATES FROM MARK-RECAPTURE DATA.
C
C REFS. JOLLY,C.M., 1965. EXPLICIT ESTIMATES FROM MARK-RECAPTURE
C DATA WITH ROTH DEATH AND IMMIGRATION - STOCHASTIC MODEL.
C RUMFRIKJA 59, P.295-87.
C PARR, M. J. 1965. A POPULATION STUDY OF A COLONY OF IMAGINAL
C ISCHNURA ELIGANS (VAN DER LINDEN) ON NATA-COINACTRIGAF
C AT DALLA, PENNSYLVANIA. FIELD STUDIES 2, 237-82.
C
C USE OF SUBROUTINE =
C CALL JOLLY (NO)
C CALL JOLLY (K,NUB)
C CALL JOLLY 2
C COMMON IOTCAP,INTREL
C NO = NUMBER OF TRAPPING CYCLES (DIMENSIONED FOR 10)
C K IS THE NUMBER OF THE PARTICULAR DAY
C NUB = A NUMBER OF THE FORM 1101, INDICATING RECAPTURES ON
C THE 1ST, 3RD, 5TH DAYS PRECEDING THIS ONE.
C IOTCAP AND INTREL ARE VECTORS OF TOTAL CAPTURES AND RECAPTURES EACH
C DAY.
C SUBROUTINES AND FUNCTIONS USED = NONE.
C *****
C DIMENSION IOTCAP(20),TOTREL(20),DAYCAP(20+20),SMRECAP(20),TIME(20)
C UTENSION Z(20),ANS(20),TRUPUP(20),AV(20),P
C COMMON IOTCAP,INTREL,TRUPUP /CUTJUL/AN,SPICAP,TEMP,ALAS,DAYCAP
C COMMON LP
C IF(NRP.EQ.1)CALL JOLLY(CAP,NRPS)
C UN 65 I=1,2U
C SRECAP(I)=0.
C Z(I)=0.
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      TEMPI)=0.
      UN 6U J=1,6
      ANS(I+J)=0.
      60 CONTINUE
      UN 65 J=1,10
      DAYCAP(I+J)=0.
      65 CONTINUE
C
C FORMAT STATEMENTS
      2U FORMAT('01234567891011121314151617181920',F10.0)
      25 FORMAT('234567891011121314151617181920',F10.0)
      30 FORMAT('234567891011121314151617181920',F10.0)
      35 FORMAT('34567891011121314151617181920',F10.0)
      40 FORMAT('4567891011121314151617181920',F10.0)
      45 FORMAT('567891011121314151617181920',F10.0)
      50 FORMAT('67891011121314151617181920',F10.0)
      55 FORMAT('7891011121314151617181920',F10.0)
      70 FORMAT('1011121314151617181920',F10.0)
      1CAPTURES CLASSIFIED BY DAY WHEN LAST CAPTURED.*///)
      60G FORMAT('1234567891011121314151617181920',F10.0)
      HTURN
C
      ENERGY JOLLY (K,NUM)
      N=NUM/10
      N8=6-1
      UN 10U J=1,K8
      L=K-J
      N8N=(N/10)+10
      IF(N8)N=90+NO
      AG DAYCAP(K,L)=DAYCAP(K,L)+1.
      NTURN
      UN 4N/10
      10G CONTINUE
      NTURN
C
      ENERGY JOLLY 2(NO,NRP,NRPS)
      N1=10L(P,55)
      N1=10L(P,70)
      N1=10L(P,60)TOTCAP(I),INTREL(I)
      I=I-1
      N1=10L(P,60)TOTCAP(I),TOTREL(I),(DAYCAP(I+J),J=1,1L)
      20G CONTINUE
C
      ACCUMULATE SUM VECTORS
      I=I-1
      N1=NO-2
      N=NO-1
      UN 25U J=1,N
      J1=J+1
      J2=J+2
      SRECAP(J)=SRECAP(J)+DAYCAP(I+J)
      23G CONTINUE
      J=I-1
      235 IF(NP(I)=TEMP(I)+DAYCAP(I+J)

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240 Z(J1)=Z(J1)+TEMP(I)
250 CONTINUE
C.
C CALCULATE POPULATION STATISTICS
C ANS(I) = PROPORTION OF MARKED ANIMALS(ALPHA)
C (P) = NO. OF MARKED ANIMALS (M)
C (Q) = POPULATION ESTIMATE (P)
C (R) = PROBABILITY OF SURVIVAL (PHI)
C (S) = NO. OF NEW ANIMALS JOINING POPULATION (B)
C (T) = STANDARD ERROR OF P
C (U) = STANDARD ERROR OF PHI
C (V) = BIAS OF ESTIMATE
C
00 300 I=2*NC
IF(TEMP(I)) 300,300,252
252 ANS(I,1)=TEMP(I)/TOTCAP(I)
254 IF(SRECAP(I))Z(I)=300.300/260
260 ANS(I,2)=Z(I)*(TOTREL(I)+1)/(SRECAP(I)+1)+TEMP(I)+1
ANS(I,3)=ANS(I,2)/ANS(I,1)
300 CONTINUE
DO 315 I=J,NC
I1=I+1
N1=N+1
IF(I1.EQ.NC)N1X=0
IF(ANS(I1,2)*ANS(I,2)*TFMP(I)*NIX) 304,304,302
302 ANS(I,4)=ANS(I+1,2)/(ANS(I,2)+TEMP(I)+TOTREL(I))
304 EM1=ANS(I,2)
EM2=ANS(I1,2)
P = ANS(I,3)
L=I
CALL JOLTOTCP(L,AR)
M1 =SRECAP(I)
M2 =SRECAP(I1)
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NA=TEMP(I1)
NR=TEMP(I1)
A1 =TOTREL(I1)
A2 =TOTREL(I1)
PHI=ANS(I,1)
IF(N1*PA*RB+R1+R2*EM1+EM2) 308,308,306
306 ANS(I,7)=PHI*2*((EM2*RR)*(EM2*RB+42)/EM2**2)*(1+RR2**1./A2)+
*(F*1-R4)/(F*1-RR+A1)*(1./R1-1./A1)*(1.-PHI)/EM2
ANS(I,7)=SORTCARB(ANS(I,7))
308 IF(C1-I)=RA*EM1*PH1 315,315,310
310 ANS(I,6)= P*(P-TOTCAP(I))*((EM1-RA+A1)/EM1)*(1./R1-1./A1)+
*(1.-ANS(I,1))/RA
ANS(I,6)=SORTCARB(ANS(I,6))
315 CONTINUE
DO 320 I=2*N8
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00 320 I=2*N8
320 ANS(I,5)=ANS(I+1,3)-(ANS(I,4)*(ANS(I,3)-TOTCAP(I)+TOTREL(I)))
C
C WRITE OUT TABLE OF RESULTS
C
C HFAOTINGS
WRITE(LP,20)
WRITE(LP,25)
WRITE(LP,30)
WRITE(LP,35)
WRITE(LP,40)
WRITE(LP,45)
C
C UOUPUT RESULTS
DO 330 I=1,N0
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924
WRITE(LP,50) I, ANS(I,1),J=1,8
330 CONTINUE
IF(CNP.LT.NREPS)RETURN
CALL JOLIT(CNRP,NS)
RETURN
EN0

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